NEW MATERIAL OF *YOUNGINA*: EVIDENCE OF JUVENILE AGGREGATION IN PERMIAN DIAPSID REPTILES

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ABSTRACT. An unusual specimen of *Youngina* is described from a new locality in the Karoo Basin of South Africa. The locality is in the *Tropidostoma* Assemblage Zone (equivalent to the former Lower *Cistecephalus* Zone), making the specimen the oldest recorded example of this genus. It comprises an association of five immature skeletons which are fully articulated and thus provide the first clear indication of body proportions in *Youngina*. In addition, the material yields new information on the pectoral girdle, pelvis and foot. It is clear that *Youngina*, unlike many of its known relatives, was an agile, fully terrestrial animal. This conclusion is reinforced by the preservation of the young skeletons in positions which suggest group denning behaviour in response to adverse climatic conditions.

YOUNGINIFORMS are a small but well-defined clade of Permo-Triassic diapsid reptiles known from the upper Permian of South Africa (*Youngina*), Tanzania (*Tangasaurus*) and Madagascar (*Hovasaurus, Thadeosaurus* and *Acerosodontosaurus*) (Gow 1975; Currie 1980, 1981*a*, 1982; Carroll 1981; Currie and Carroll 1984), and from the lower Triassic of Kenya (*Kenyasaurus*; Harris and Carroll 1977). Once thought to be related to lepidosaurs (lizards, snakes and their relatives) (e.g. Evans 1988), younginiforms are now placed closer to the base of the diapsid tree (Laurin 1991).

The genus *Youngina* was erected by Broom (1914) on the basis of a single skull, now in New York (AMNH 5561). Further specimens followed (e.g. Broom 1922), but many of these were assigned to new genera and species (*Youngopsis kitchingi* Broom, 1937; *Youngoides rowei* Olson and Broom, 1937; *Youngopsis rubidgei* Broom and Robinson, 1948 and *Youngoides minor* Broom and Robinson, 1948). Gow (1975) published the first comprehensive review of the known cranial and postcranial material, and concluded that all specimens could be referred to a single genus and species, *Youngina capensis*.

Youngina has often been considered to be an archetypal Permian diapsid, but its morphology remains incompletely known. As with all small diapsid reptiles, the fossil record of younginids in the Karoo Basin of southern Africa is comparatively sparse. There are 13 known skulls, only one of which (BPI 3859) has an associated postcranial skeleton. This skeleton is incomplete (missing parts of the fore- and hindlimbs and pectoral girdle) and was disarticulated to permit detailed description of individual bones (Gow 1975). Furthermore, all the *Youngina* specimens collected so far are from Beaufort Group strata assigned to the *Dicynodon* Assemblage Zone (Kitching in press). Previously termed the *Daptocephalus* Zone (Kitching 1977), these strata are considered to be of uppermost Permian age (Anderson and Cruickshank 1978).

Recently, one of us (RMHS) recovered an unusual specimen of *Youngina* from 700 m lower in the Beaufort succession than previous finds. The new locality is in the *Tropidostoma* Assemblage Zone (Smith and Keyser in press) which is equivalent to the former lower *Cistecephalus* Zone of Kitching (1977) (Smith and Keyser in press). The specimen, designated SAM K7710, in the collections of the South African Museum, Cape Town, is thus some 2·3 My older than other known specimens. It contains five fully articulated immature *Youngina* skeletons (plus a hindlimb of one other) preserved in attitudes and orientations that strongly resemble those of modern lizards when displaying group denning behaviour.
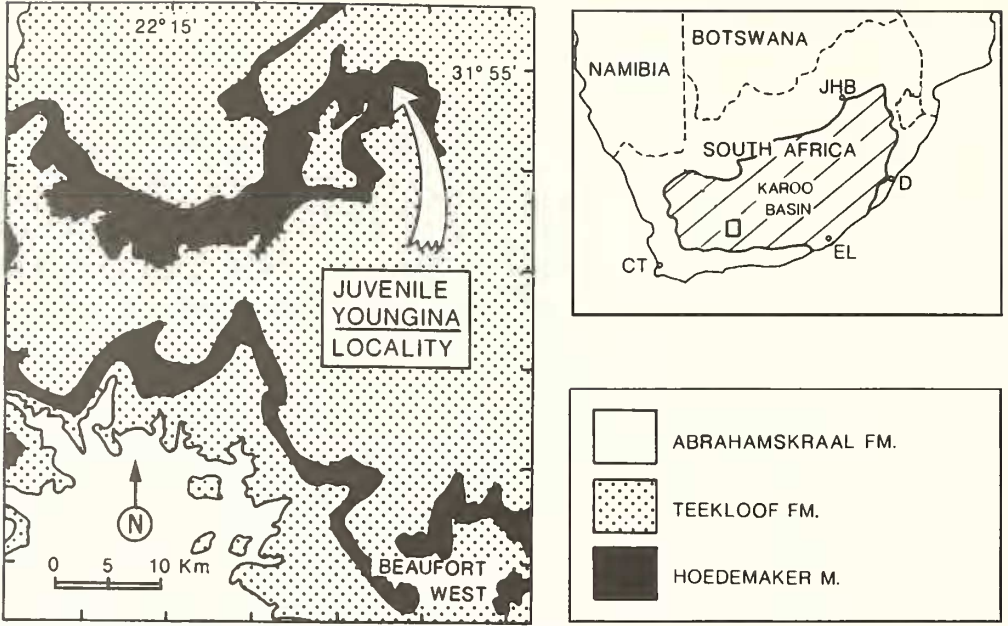
TEXT-FIG. 1. Lithostratigraphy of the area surrounding the new younginid fossil locality (SAM K 7710) in the south-western Karoo Basin.
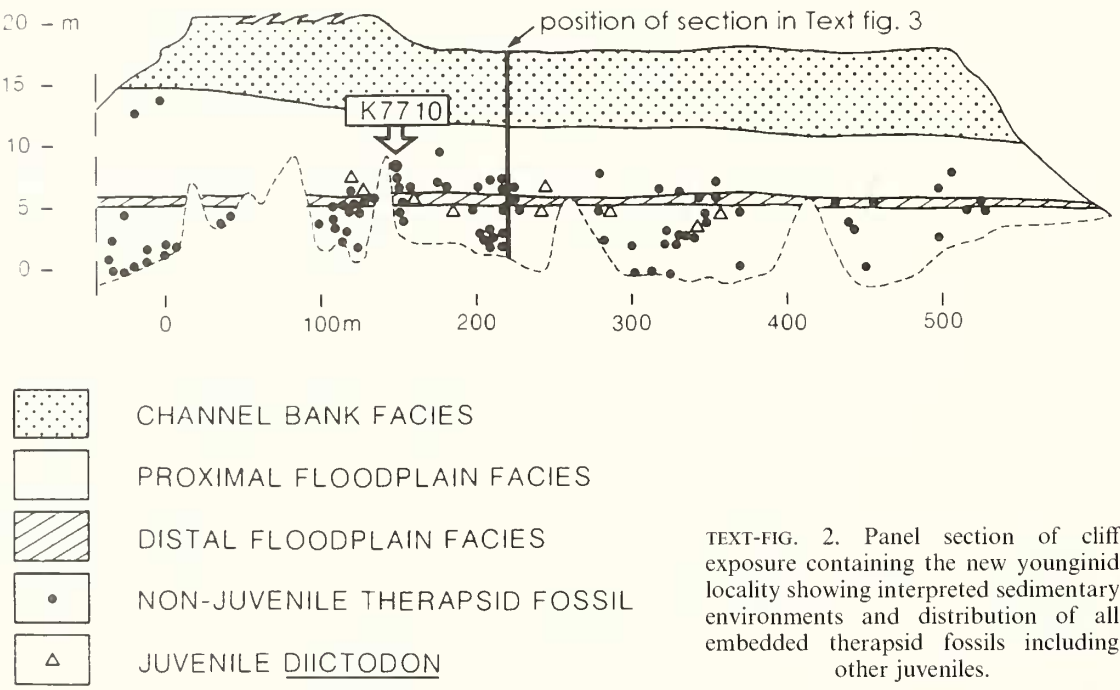
TEXT-FIG. 2. Panel section of cliff exposure containing the new younginid locality showing interpreted sedimentary environments and distribution of all embedded therapsid fossils including other juveniles.

The aims of this study are to describe the significant morphological features and juvenile characteristics of these skeletons, and to investigate their taphonomic history through sedimentological analysis of the host sequence.
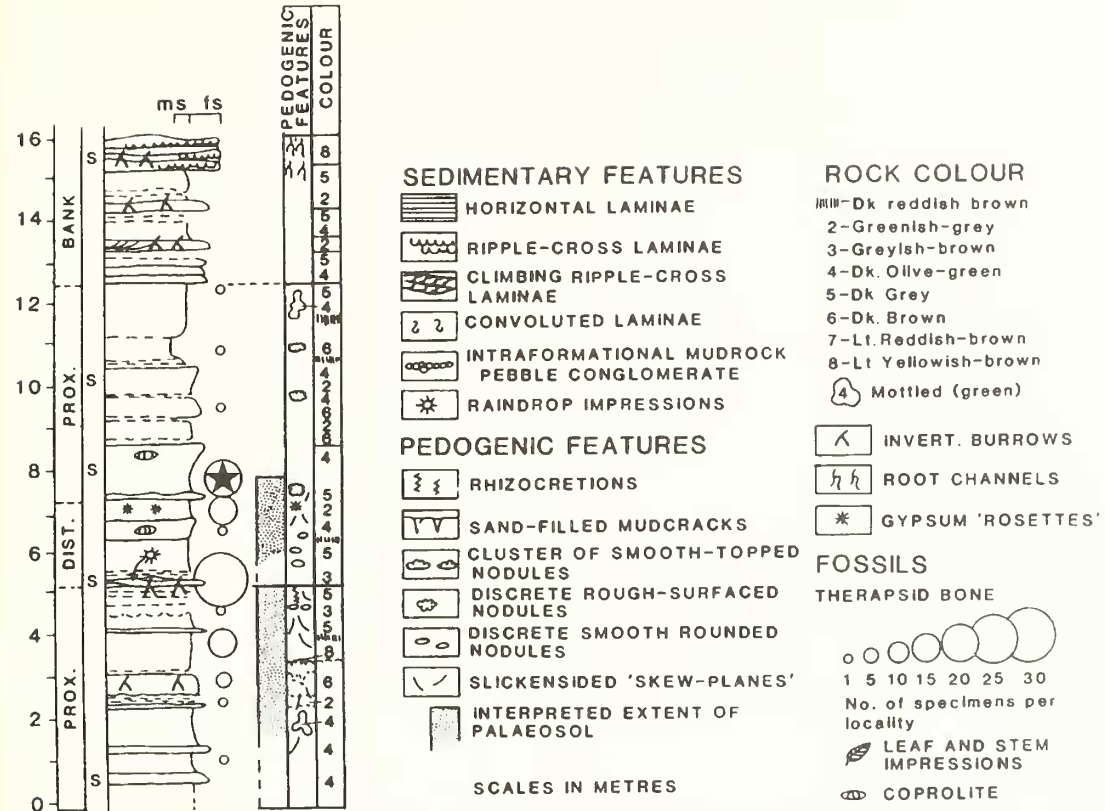
TEXT-FIG. 3. Columnar section at new younginid locality showing details of lithology, sedimentary structure, palaeosols and fossils.

Institutional abbreviations: AMNH – American Museum of Natural History, New York; BPI – Bernard Price Institute of Palaeontology, Johannesburg; KNM – Kenya National Museum, Nairobi; MNHN – Muséum National d'Histoire Naturelle, Paris; SAM – South African Museum, Cape Town; TM – Transvaal Museum, Pretoria.

THE SEDIMENTARY ENVIRONMENT OF THE *YOUNGINA* LOCALITY

The new *Youngina* locality is on the border between the Beaufort West and Loxton districts of the Cape Province of South Africa, within a regionally extensive mudrock sequence, the Hoedemaker Member, which makes up part of the Teekloof Formation of the Beaufort Group (Adelaide Subgroup) in this area (Text-fig. 1). The Hoedemaker mudrocks form the upper part of a large fining-upward megacycle. Several of these 150–450 m thick first order cycles were deposited in a foreland trough by northerly flowing drainage nets. They formed in response to increased subsidence in the foreland basin which was probably synchronous with renewed thrusting in the rising 'Gondwanide' orogenic belt. The basal, predominantly channelized, portion of the megacycle (the Poortjie Sandstone Member) consists of multistoried and multilateral medium to high sinuosity meander-belt sandstone bodies with interbedded overbank mudrocks in ratios of up to 1:2. The overlying Hoedemaker Member has channel to overbank ratios of 1:4–1:6 and has been described as a 'floodplain facies association' (Turner 1978) with sedimentation dominated by unconfined sheet flow, and suspension settling in ponds and lakes.
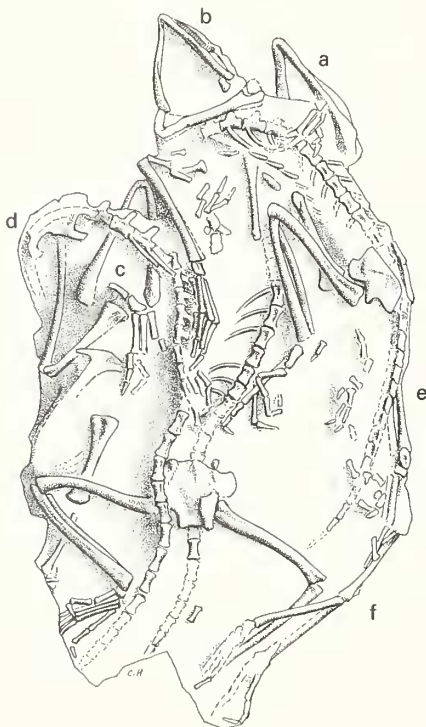
Previous research on the Hoedemaker mudrocks involving detailed mapping of sedimentary facies and palaeosols, and taphonomic analysis of embedded vertebrate fossils, has led to the
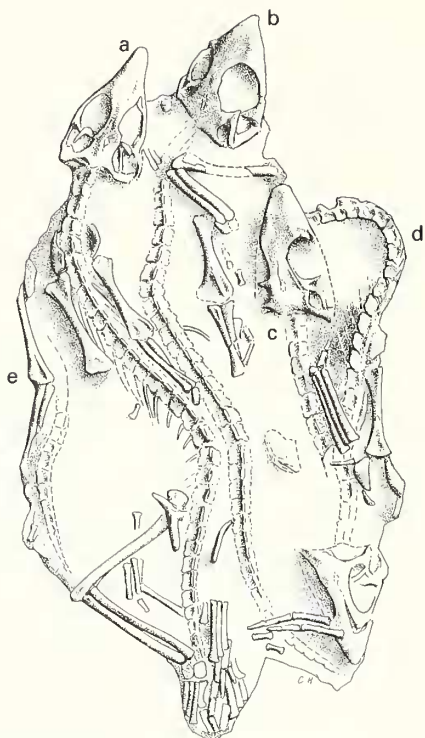
recognition of various sedimentologically defined floodplain environments (Smith 1993). The *Youngina* specimen was found during a systematic search for every embedded fossil that was visible in a 1300 m long by 15 m high cliff section exposure (Text-fig. 2). A total of 243 *in situ* fossils were located, mostly skulls and postcrania of small herbivorous dicynodonts such as *Diictodon*, *Pristerodon*, *Emydops* and *Oudenodon*. The younginid fossil was found in a sequence of drab grey, greenish grey and maroon mudrocks with interbedded light brown fine-grained sandstone sheets. It was embedded in a 2 m thick structureless greenish-grey siltstone which contained no evidence of pedogenic alteration (Text-fig. 3). The host sequence is interpreted as having accumulated on the proximal floodplain areas flanking a large Mississippi-sized meandering river (Smith 1987*a*). Sedimentary structures in the point bars making up the main channel sandstones in this sequence indicate that the river was perennial and prone to large discharge fluctuations resulting in flood dominated sedimentation (Stear 1985). The structureless siltstone in which the younginids were buried is interpreted as sheetflood alluvium, rapidly deposited by sediment-laden floodwaters which overtopped the channel banks and then flowed as an unconfined sheet down the meander-belt ridge and across the proximal floodplain (Smith 1980).

Calcic palaeosols in the associated sediments (see Text-fig. 3) confirm that floodplain sedimentation was highly episodic and semi-arid climatic conditions prevailed in this part of the basin. Comparison of the palaeosol profiles with those of modern soils allows estimates of mean annual temperatures, of between 16 °C and 20 °C, and highly seasonal rainfall, of 500–700 mm/y (McPhereson and Germs 1979; Smith 1990). The distribution of rooted horizons is evidence that vegetation flourished along riverbanks and abandoned channel furrows and consisted of *Glossopteris* trees, horsetails, ferns and clubmosses (Rayner 1992). This supported a stable terrestrial vertebrate fauna dominated by a variety of therapsids, the fossils of which are common enough to be used as biostratigraphical indicators throughout the Beaufort succession. When found, the new younginid specimen (SAM K7710) was completely encased in a thin layer (5 mm) of micrite-cemented siltstone. Such preferential peri-mineralization of fossil bone is common in the proximal floodplain facies of the Hoedemaker Member and is interpreted to be of early diagenetic, probably pedogenic origin.

DESCRIPTIVE PALAEONTOLOGY

The five younginid skeletons are preserved in a dorsalside-up attitude along the floor of a shallow depression. Their skeletons are superimposed (Text-figs 4–5), but show no evidence of disturbance other than that attributable to vertical compaction. The high degree of articulation of these delicate skeletons and the presence of free-floating sternal plates indicates that they were buried with their flesh intact. This, coupled with the spatial arrangement of limbs and the parallel orientation of the skeletons in a dish-shaped depression, is compelling evidence for them having been preserved in 'life position' as a behaviourally arranged aggregation of young animals within an underground burrow.

Both dorsal and ventral surfaces were prepared mechanically with dental drill and needle under magnification. Anatomical details were recorded on transparent film using radiographs to maintain positional accuracy. These drawings were then enlarged in a photocopier and reversed onto clear film making it possible to superimpose dorsal-on-ventral views (and vice versa) in order to reveal the intricacies of their taphonomy (Text-fig. 4A–D).

To aid identification in the descriptive section that follows, the articulated skeletons have been coded a–e (Text-fig. 4B–C); f is an isolated hindlimb from another individual.

Identification and ontogenetic age

The five articulated individuals are of closely similar size (snout-vent length 87–95 mm) and are of roughly the same level of skeletal development. In the skull, several features (the elongated posterior process of the post-orbital; the U-shaped configuration of the fronto-parietal suture; the rod-like

TEXT-FIG. 4. *Youngina capensis*; SAM K7710. A–B, the dorsal surface; C–D, the ventral surface. a–f mark individuals as described in the text. Scale bar represents 10 mm.

TEXT-FIG. 5. Fleshed-up reconstruction of the juvenile younginids shortly after their death some 255 Ma.

quadratojugal contacting the jugal below the lower temporal fenestra) identify these animals as younginiforms. This is further corroborated by the short neck (four or probably five cervicals), the form of the vertebrae (midline accessory processes), the structure of the pectoral girdle (long-stemmed interclavicle, sternal plates) and the shape of the distal head of the humerus (well-developed entepicondyle).

In the detailed pattern of preserved skull elements e.g. narrow premaxilla, parietal shape (posterior process angle and orientation; tabular and supratemporal facets), slender dentary; the dentition (tooth shape, maxillary and dentary tooth counts of 20–22 and 19–20 respectively); and in most features of postcranial anatomy (e.g. broad, nearly horizontal dorsal zygapophyses; low rectangular neural spines; the shape of the fifth metatarsal), these small skeletons show no marked morphological differences from previous descriptions of the genus *Youngina* (e.g. Goodrich 1942; Gow 1975). They are, however, only about half the size of other specimens, although many of these are immature (Currie 1981*a*).

The skeletons on SAM K7710 are too well ossified to represent hatchlings. The neurocentral sutures are closed; tarsal and carpal elements are at least partially ossified; the components of pectoral and pelvic girdles are in close proximity (i.e. there were no large areas of cartilage separating them); and the sacral and caudal ribs are fused to their respective vertebrae (although there remains a trace of a suture on one individual). However, there is also evidence that these small reptiles were immature. In the skull, the roofing bones are unsculptured; the paired frontals and parietals are joined by simple sutures and the bones have separated easily; the postorbital bar is slender; and the eyes and the parietal foramen are proportionally large. In the postcranium, the sternal plates are only weakly ossified and remain paired, although the coracoid foramen is already enclosed and the scapula and coracoid appear to have fused; the pubis and ischium are separated by a weakly ossified area and are commonly notched (giving the appearance of a small thyroid fenestra); the obturator foramen of the pubis is open posteriorly in some individuals; and the ends of the long bones lack well-formed joint surfaces. There is no trace of the dermal armour seen in the postcranial skeleton described by Gow (1975) (BPI 3859). The carpals and tarsals appear incompletely preserved and there is no trace of a notch on the calcaneum or astragalus for a perforating artery.

Developmental stages have been described for two other younginiforms, *Hovasaurus* (Currie 1981*a*) and *Thadeosaurus* (Currie and Carroll 1984). *Hovasaurus* was almost certainly aquatic whilst *Thadeosaurus* is thought to have been more terrestrial. Currie (1981*a*) divided his specimens of *Hovasaurus* into a series of age classes from A (hatchling) to H (fully mature adult) on the basis of growth increments, and the same system was used for *Thadeosaurus* (Currie and Carroll 1984). Allowing for the difficulties of comparing aquatic animals with terrestrial ones, and the absence of a full series for *Youngina*, the small younginid skeletons on SAM K7710 would seem to correspond with age class D/E in the Madagascan genera. The sequence of ossification, however, may have been slightly different. Currie (1981*a*), for example, reported that the obturator foramen of the pubis is fully enclosed by stage B in *Hovasaurus*, when the neurocentral sutures are still open. In the young skeletons on SAM K7710, the neurocentral sutures are closed but the obturator foramen is open in several individuals (K7710e for example).

Morphology

Skull and vertebrae. The skull of *Youngina* is well-known through the work of Gow (1975), and SAM K7710 serves only to confirm details of previous accounts. Gow (1975) described the only associated postcranial skeleton of *Youngina capensis* (BPI 3859) as 'jumbled together in a tight bundle behind the skull' with part of it already rotted away. He estimated that only the atlas, axis and sacral 1 had been lost, giving a presacral count of 23, of which four were cervical. SAM K7710a, however, suggests that there were at least 24 presacrals, probably with five in the neck.

The atlas/axis complex is partially exposed in SAM K7710a. The atlas is eroded but the axis spine is anteroposteriorly extended and there appears to be a small double-headed axial rib (as in *Hovasaurus* Currie, 1981*a*).

Details of vertebral structure are given by Gow (1975) and Currie (1981*b*) and need not be repeated here. As preserved, the vertebrae of SAM K7710 accord with previous descriptions. As in other younginiforms, the last five or six presacral ribs are very short. The sacrum is preserved in SAM K7710d; sacral 1 is robust with a rounded end, sacral 2 and caudal 1 match those figured by Gow (1975), although their tips are damaged. The tail is long with anterior caudals (about 12) bearing strong transverse processes for the caudifemoral muscles. Deep haemal spines begin on the second or third postsacral (a shorter pygal region than that suggested by Gow 1975).

Pectoral girdle and forelimb. Broom (1921) and Gow (1975) described briefly and figured parts of the pectoral girdle and forelimb (from TM 200 and BPI 3859 respectively). Broom's material suggested the presence of small paired sternal plates (as in other younginiforms) and this is confirmed in SAM K7710. By comparison with other genera, these plates presumably fused in the adult.

Several of the individuals on SAM K7710 preserve elements of the pectoral girdle and permit a rather more detailed description and reconstruction of this region (Text-fig. 6c). K7710a reveals only the dorsal parts of
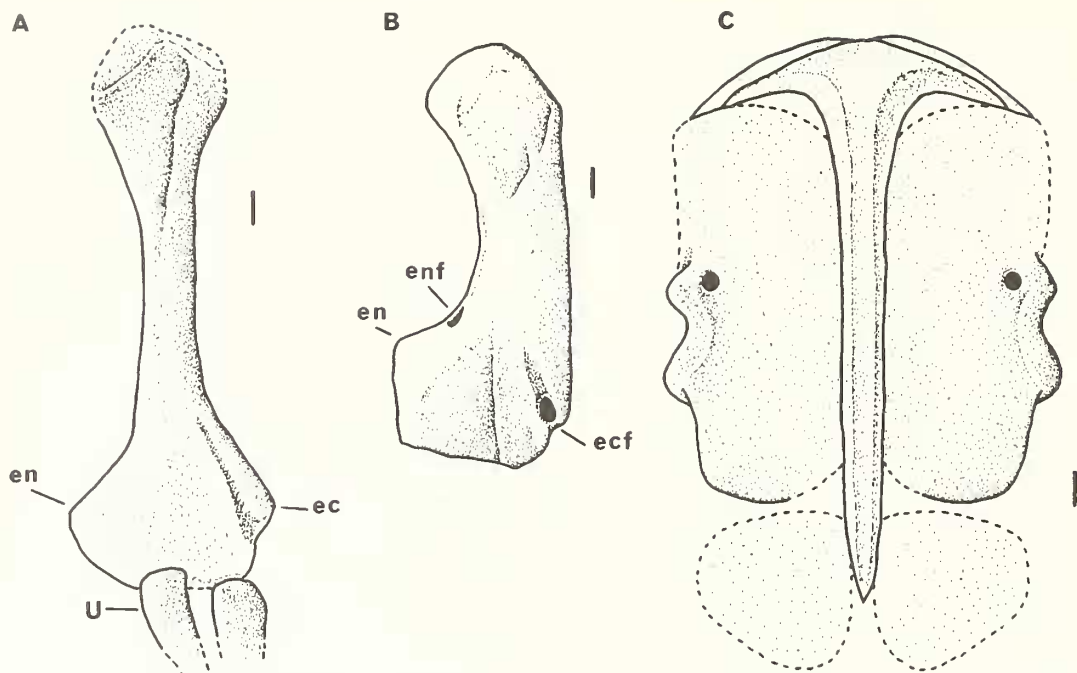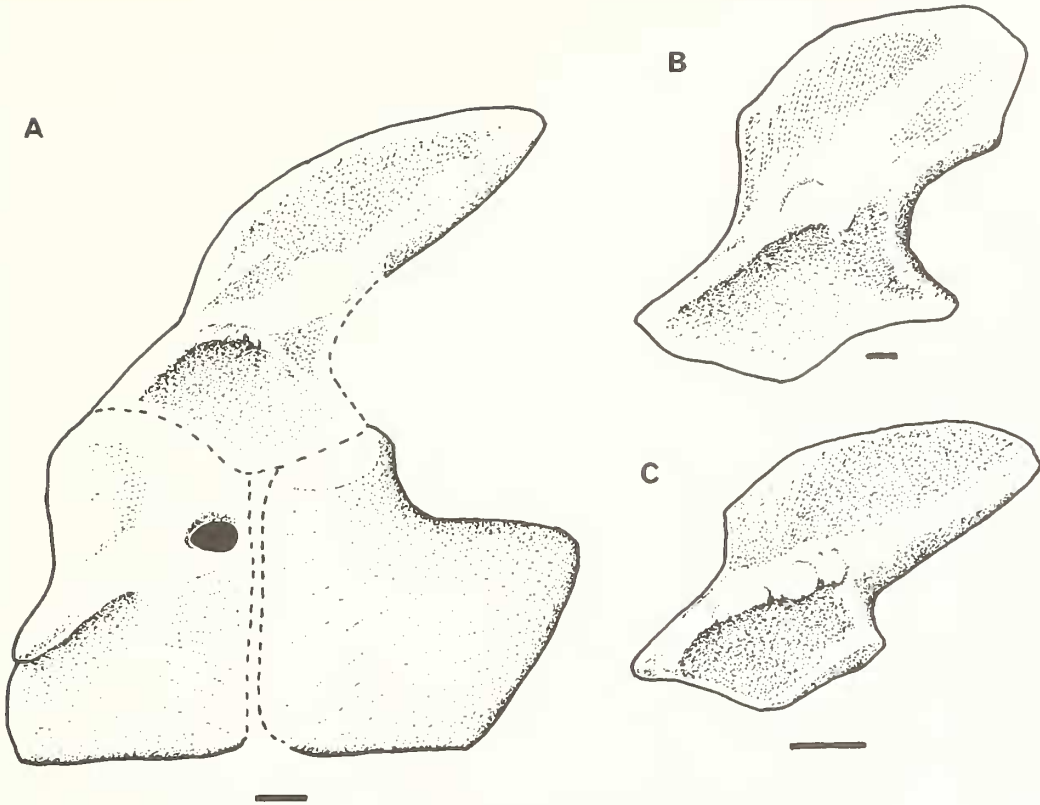
TEXT-FIG. 6. A, *Youngina capensis*, SAM K7710, reconstruction of the left humerus in dorsal view, based mainly on SAM K7710b and e; B, *Hovasaurus boulei*, reconstruction of humerus in dorsal view (redrawn and reversed from Currie 1981a, fig. 25); C, *Youngina capensis*, SAM K7710, reconstruction of the pectoral girdle in ventral view. Scale bars: A, C represent 1 mm; B represents 5 mm. Abbreviations: ec, ectepicondyle; ecf, ectepicondylar foramen; en, entepicondyle; enf, entepicondylar foramen; U, ulna.

the scapulae, supporting Gow's (1975) reconstruction of a tall blade, which contrasts with the shallower condition in related aquatic genera (e.g. Currie 1981a). The clavicle is preserved in several individuals, but is seen best in K7710a. It is a robust sickle-shaped element with no indication of facets or notches to suggest the presence of a cleithrum (*contra Acerosodontosaurus* Currie, 1980 and *Hovasaurus* Currie, 1981a), although the absence of a cleithrum cannot be taken as certain. Ventrally, the coracoid plate appears to be more extensive than shown in Gow's figure (1975, fig. 9c). The coracoid foramen is fully enclosed in K7710a and the glenoid is large. The head of the interclavicle is broadly T-shaped, as illustrated by Gow (1975), but the stem is long (extending the length of about six trunk vertebrae) and supports both the posterior extensions of the coracoids and the sternal plates (Text-fig. 6c). This resembles closely the condition in other younginiforms (Harris and Carroll 1977; Currie 1981a).

Most individuals on the SAM K7710 block have elements of the forelimbs preserved. The humerus is preserved on several individuals, and appears as a long, rather slender bone (Text-fig. 6A), ranging in length from 15–17 mm (5–5·7x, where x is the length of a dorsal centrum, a standard used by Currie 1981a). The humeral shaft is twisted so that proximal and distal ends lie at an angle to one another (though at rather less than 90°). The proximal end is narrower than the distal and its dorsal surface bears a distinct depression (corresponding to the insertion of the scapulohumeralis muscle in other taxa; Currie 1981a). The distal end is very similar to that of BPI 3859, as described by Gow (1975). It bears an expanded entepicondyle (although less developed than in related genera, e.g. *Hovasaurus*; Text-fig. 6B). This region is pierced by an entepicondylar foramen, but the foramen opens laterally and is not clearly visible in dorsal view. There is an ectepicondylar groove but, at least at this developmental stage (and that of BPI 3859), no ectepicondylar foramen.

The radius and ulna are preserved most clearly in K7710e; they are substantially shorter (70–73 per cent.) than the humerus. According to Gow (1975), the radius of BPI 3859 is somewhat longer than the ulna (18:16 mm), a condition seen in the adults of derived younginiforms, but not in *Acerosodontosaurus* (Currie 1980). However, in immature individuals, this difference can be negligible (e.g. *Thadeosaurus* Currie and Carroll, 1984). In SAM K7710, the radius and ulna are exposed together only in individuals d and e. The

TEXT-FIG. 7. A–B, *Youngina capensis*. A, SAM K7710; reconstruction of the pelvic girdle in left lateral aspect (based mainly on SAM K7710a + e). B, BPI 3859; lateral view of left ilium (drawn from original). C, *Acerosodontosaurus piveteaui*; MNHN 1908-32-57; lateral view of left ilium (redrawn from Currie 1980, fig. 7B). Scale bars: A–B represent 1 mm; C represents 5 mm.

elements appear to be of roughly equal length (3·5x), but allowing for the age of the individuals, and the imperfect preservation of the proximal and distal ends, this is not significant. As in other younginiforms, however, the radius is slightly twisted.

None of the wrist and hand elements is clearly preserved. They serve only to support Gow's (1975) general reconstruction of a rather sturdy hand with digits substantially shorter than those of the foot. As in the foot, however, the first and fifth metacarpals appear to be shorter and more robust than those of the intervening digits (seen also in BPI 3859, although not obvious in Gow's fig. 9A). Each claw bears a strong flexor tubercle.

Pelvic girdle and hind limb. Gow (1975) figured a complete pelvis with a notch between the pubis and ischium, interpreting the notch as being due to incomplete ossification rather than an incipient thyroid fenestra. SAM K7710 supports this view. In K7710e, for example, the notch is larger than that shown in BPI 3859 and, anteriorly, incorporates the obturator foramen; in K7710b, ossification is a little more advanced and there is bone filling the puboischiadic notch. The pubis and ischium are short and robust (Text-fig. 7). The former bears a strong pectineal tuberosity and is somewhat inflated anteriorly, both conditions seen in other younginiforms. The ilia are best preserved in K7710a and K7710e. These individuals show the iliac blades to be more attentuated and horizontal than those in Gow's reconstruction (1975, fig. 9d). As preserved, there is certainly a difference in the shape of the blades in BPI 3859 (Text-fig. 7B) and SAM K7710a + e (Text-fig. 7A). However, allowance must be made for the difference in size of the animals, the uncertainty with respect to the shape of the posteroventral margin in SAM K7710, and the possibility that the blade of BPI 3859 is incomplete posterodorsally. Removing the posterior tip from the iliac blade of *Acerosodontosaurus* (Text-fig. 7C), for example, would leave an ilium of a shape similar to that of BPI 3859.

In BPI 3859 the hind limb elements are restricted to a femur, a partial tibia and a fourth metatarsal. By

contrast, the hind limbs are well preserved in several individuals on SAM K7710. The femora are long (6·3–7x) and slender, without conspicuous muscle attachments (possibly age-related). The tibia and fibula are also long (6·3–6·7x), with the tibia slightly longer and broader than the fibula.

The ankle is missing in BPI 3859, but was described and figured by Broom (1921) and Goodrich (1942); according to Gow (1975), this material is now lost. In SAM K7710, parts of the ankle are preserved in several individuals (Text-fig. 8A). The proximal tarsal row consists of a large, subtriangular astragalus (intermedium
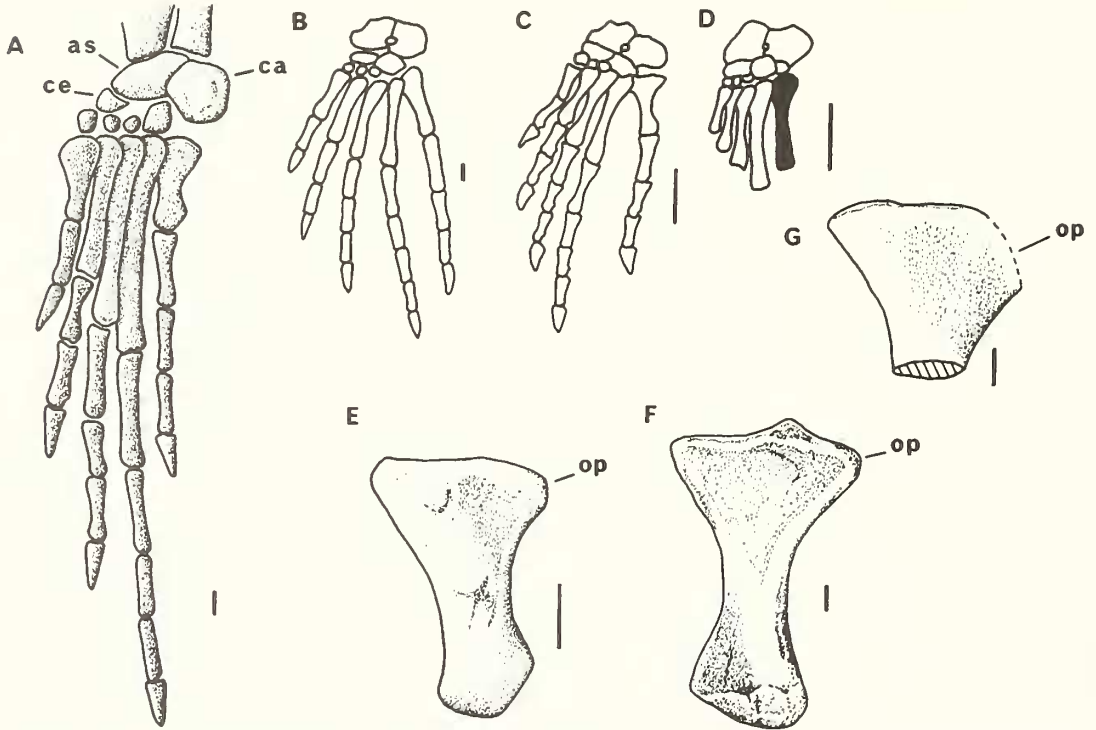
TEXT-FIG. 8. A, *Youngina capensis*, SAM K7710, reconstruction of left foot in dorsal view (based mainly on SAM K7710a); B–D, for comparison, reconstructions of the same foot in B, *Hovasaurus boulei* (redrawn from Currie 1981a, and based on more than one specimen); C, *Kenyasaurus mariakaniensis* KNM Ma1 (redrawn from Harris and Carroll 1977); D, *Youngina capensis*, TM 200 (redrawn from Broom 1921). E, *Youngina capensis*, SAM K7710d, right fifth metatarsal in plantar view. F, *Kenyasaurus mariakanensis*, KNM Ma1, right fifth metatarsal in plantar view (redrawn from Harris and Carroll 1977). G, *Youngina capensis*, TM 200, the proximal head of the fifth metatarsal as drawn by Goodrich (1942; reversed to aid comparison). Scale bars: A, E–G represent 1 mm; B–D represent 10 mm. Abbreviations: as, astragalus; ca, calcaneum; ce, medial centrale; op, outer process.

of Broom) which carries facets for the tibia and much of the fibula; laterally it overlaps an almost square calcaneum (fibulare of Broom). Distal to the astragalus is a medial centrale (tibiale of Broom), but the precise size, shape and relations of this bone cannot be determined. The distal tarsal row bears at least four elements (the presence or absence of DT5 cannot be confirmed) of which DT4 is the largest.

The foot is asymmetrical with digit 4 longest (Metatarsal 4, 3–3·3x). The fifth metatarsal is essentially straight but has an expanded proximal head with a conspicuous outer process for the peroneus brevis muscle (Text-fig. 8E). In length, the fifth metatarsal is intermediate between the first and second (Table 1). This interpretation differs from that of Broom (1921, figs 19–20; Text-fig. 8D), who described, and reconstructed the element as being 'a long slender bone, nearly as long as the fourth metatarsal'. Goodrich's (1942, p. 311) account of the same element, based on the original specimen, differs markedly. The bone is described as being considerably shorter than the fourth metatarsal and as having a very broad proximal head (as shown in his accompanying figures and photograph; Text-fig. 8G). Clearly, the shaft of the fifth metatarsal was broken just distal to the

proximal head; Broom's reconstruction relied on impressions which must have included the proximal phalanx. The known specimens of *Youngina* are thus closely comparable. All mature younginiforms show some widening of the proximal head of the fifth metatarsal, but, apart from *Youngina*, it is most marked in *Kenyasaurus* (Harris and Carroll 1977; Text-fig. 8F). The phalanges are generally short and robust, with strong unguals; the phalangeal formula is 2:3:4:5:4.

Body and limb proportions. The preservation of the skeletons with the limbs fully articulated permits better estimation of body proportions, even allowing for subsequent changes during growth. Table 1 gives details of

TABLE 1. Body proportions in SAM K7710, individuals a–f (all lengths in mm).

	a	b	c	d	e	f
Snout-vent length	89	95	—	87	—	—
Skull length	21	21	22	20	—	—
Humerus	16·5	17	16	14+	15	—
Radius	—	—	—	11	10·5	—
Ulna	—	—	—	11	10·5	—
Femur	18·5	21	—	19	19	13+
Tibia	18·5	20	—	18	19	11+
Fibula	17·5	20	—	—	18	—
MT5	4·5	4	—	—	—	—
MT4	10	—	—	9	—	—
MT3	8·5	7·5	—	7·5	—	—
MT2	6	6·5	—	5·5	—	—
MT1	—	3	—	3	3	—
Reconstructed foot	30	—	—	25+	30	—
Mid trunk centrum	—	3	—	—	3	—
Interclavicle length	—	—	16·5	—	—	—
Tail	—	—	—	90+	78+	—

the lengths of individual elements, while Table 2 provides a comparison between SAM K7710 and other younginiforms.

The young skeletons on SAM K7710 are characterized by their long hind limbs (75 per cent. of snout-vent length), in which all elements, femur, tibia and foot, are elongated. The forelimb is much shorter (around 58 per cent. of the hind-limb length).

SAM K7710 is very similar to BPI 3859 in the relative lengths of the radius, the femur and the fourth metatarsal. The two main differences relate to the lengths of the humerus and the tibia, both of which appear shorter in BPI 3859. The tibia, however, is incomplete in BPI 3859 and was reconstructed by Gow (1975) on the basis of the fragmentary remains of TM 200. Allowing for some underestimate, and the ontogenetic age difference between the *Youngina* specimens, the differences are not significant. In general, the lengths of the radius and tibia are remarkably consistent in younginiforms (Table 2).

The differences in the humerus length, however, are rather greater. Laurin (1991) commented on the unusually short humerus in *Youngina*, but the humeri of SAM K7710 are comparable in length to those of other younginiforms. There are three possible explanations for the differences between BPI 3859 and SAM K7710: there is a genuine, taxonomically significant length disparity; the humerus of BPI 3859 is incomplete; or humeral growth lags behind that of other limb elements in *Youngina*. A combination of the last two alternatives seems most likely. In this case, the humerus of *Youngina* would show a growth pattern the reverse of that in *Hovasaurus* (Currie 1981a) and *Thadeosaurus* (Currie and Carroll 1984) where humeral growth is accelerated in relation to other limb elements, leaving the humerus of equal, or greater, length than the femur in the mature adult. Furthermore, the difference between BPI 3859 and SAM K7710 in their humerus/femur ratios (10–20 per cent.) is greater than that between their radius/humerus ratios (8 per cent.), suggesting that accelerated growth of the femur may also have played a part. Growth processes in *Youngina* would therefore have tended to increase the forelimb/hindlimb disparity (as might be expected in a terrestrial cursor) whilst in *Hovasaurus*, they tended to decrease it (as might be expected in a swimmer, although this does not explain the condition in the supposedly terrestrial *Thadeosaurus*).

TABLE 2. Body proportions of Younginiformes. x, length of dorsal vertebra; F, femur; H, humerus; Mt, metatarsal; R, radius; T, tibia. Data from Harris and Carroll 1977; Currie 1980, 1981a, 1982; Carroll 1981; Currie and Carroll 1984. *indicates proportions affected by estimate of tibial length.

	Hx	Fx	Rx	Tx	Mt4x	Mt5x	Footx	
Acerosodontosaurus	—	6·1	3·8	—	—	—	—	
Youngina SAM K7710	5–5·7	6·2–7	3·7	6·2–6·7	3–3·3	1·3–1·5	10	
Youngina BP1 3859	4·6	6·8	3·6	5·6*	3·4	—	—	
Kenyasaurus	5·3	5·8	—	5·1	2·8	1·9	9·2	
Thadeosaurus (Stage B)	5·0	6·7	3·5	5·8	3·2	2·8	12·1	
Thadeosaurus (Stage D)	5·1	6·2	3·7	5·4	3·1	2·6	—	
Thadeosaurus (Stage G)	6·1	6·2	3·7	—	—	—	—	
Tangasaurus	5·5	6·3	3·5	5·5	2·8	2·3	9·5	
Hovasaurus (Stage B)	4·2	4·9	2·8	4·1	2	1·4	6·7	
Hovasaurus (Stage G)	6·9	6·2	3·9	5·5	—	—	—	
	Dig4x	Dig5x	R/H %	T/F %	H/F %	R/T %	Mt5/4 %	Dig5/4 %
Acerosodontosaurus	—	—	—	—	—	—	—	—
Youngina SAM K7710	8	4·5	70	95–100	79–89	61	45	57
Youngina BP1 3859	—	—	78	89*	68	59*	—	—
Kenyasaurus	7·7	6	—	87	91	—	68	78
Thadeosaurus (Stage B)	10·1	7·5	70	87	75	60	79	83
Thadeosaurus (Stage D)	—	—	65	87	83	62	83	—
Thadeosaurus (Stage G)	—	—	60	89	97	66	—	—
Tangasaurus	8	7·3	66	85	89	63	82	91
Hovasaurus (Stage B)	6·1	5·3	66	84	85	67	80	89
Hovasaurus (Stage G)	—	—	52	85	110	73	—	—

As reconstructed, the foot of *Youngina* also differs from that of other younginiforms in the proportions of the fourth and fifth digits. While the fourth metatarsal is of similar length in all taxa (with the possible exception of *Hovasaurus*), the fifth metatarsal is relatively shorter in *Youngina*, as is the complete fifth digit. The result is a more asymmetrical foot. In *Hovasaurus* and *Tangasaurus*, the fifth digit approaches the fourth in length (89 per cent. and 91 per cent. respectively), while the condition in the less specialized *Kenyasaurus* and *Thadeosaurus* is intermediate (78 per cent. and 83 per cent. respectively). Elongation of the fifth digit may have improved the effectiveness of the foot as a paddle, although without evidence of the foot structure in *Acerosodontosaurus*, the polarity of this character within younginiforms is difficult to assess. In general, however, a short fifth pedal digit appears to be primitive for diapsids; the fifth digit is 61 per cent. of the fourth in, for example, the late Carboniferous *Petrolacosaurus* (Reisz 1981).

DISCUSSION

This is the earliest recorded occurrence of *Youngina* in the Karoo Supergroup, with an estimated age of middle to upper Tatarian (250–255 Ma) based on correlation of the associated *Tropidostoma/Endothiodon* fauna with similar fossils in the Rio do Rasto Formation of Brazil (Keyser 1981). These specimens are the only completely articulated and undistorted skeletons of *Youngina* to have been discovered to date.

Relationships. SAM K7710 bears a strong resemblance to previously described material of *Youngina capensis*, differing only in the shape of the iliac blade and in the proportions of the humerus; both differences could be due to a combination of preservation and growth changes. Considering the geological age difference between the specimens, they may have been specifically distinct, but there are inadequate morphological grounds on which to base a new species and the individuals on SAM K7710 must be referred to *Youngina* cf. *capensis*.

These new specimens add to our knowledge of the morphology of the genus and aid comparison with other younginiforms. As concluded by Currie (1982) and Evans (1988), *Youngina* appears to have been distinct from the tangasaurs (*Hovasaurus*, *Tangasaurus*, *Kenyasaurus* and *Thadeosaurus*) which are linked by a number of derived features (Currie 1981a; Evans 1988; Text-fig. 9) including

TEXT-FIG. 9. Cladogram showing generally accepted relationships of the younginiform genera (based on Currie 1982 and Evans 1988). Nodes: (1) short neck with 4–5 cervicals; postorbital bone with posterior process reaching posterior margin of upper temporal fenestra; reduced, rod-like quadratojugal meeting jugal below lower temporal fenestra; enlarged humeral entepicondyle. (2) accessory articulation facets on neural spines; paired sternal plates which co-ossify in mature adult; radius longer than ulna in mature adult. (3) Tangasauridae: humerus = or > femur; radius 50–65 per cent. humerus length; medial centrale of wrist meets distal carpal 4; medial centrale of wrist = 2 × lateral centrale; first distal tarsal enlarged; fifth distal tarsal lost or fused; humeral entepicondyle greatly enlarged; scapula blade low; scapula subequal to coracoid. (4) 19–28 pairs of caudal ribs and transverse processes present. (5) high dorsal and caudal neural spines; 9–12 pairs of caudal ribs; anterior caudal ribs expanded distally; haemal spines enlarged and plate-like.
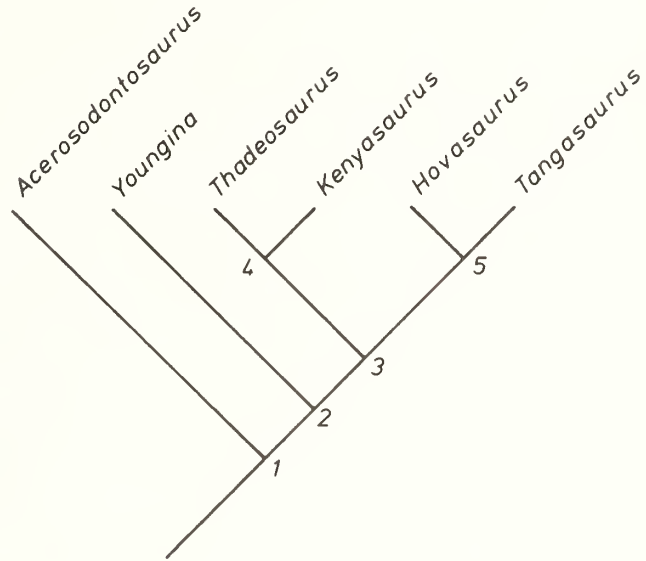
a more pronounced expansion of the entepicondylar region of the humerus and an apparent elongation of the fifth digit in relation to the fourth (Text-fig. 7B–C). In the absence of accessory processes on its vertebral neural spines, *Acerosodontosaurus* (Currie 1980) appears to lie at the base of the group, although its incomplete preservation limits its usefulness as an outgroup for *Youngina* and the tangasaurs.

Lifestyle. The lightly built, long-limbed skeletons provide evidence that *Youngina*, unlike its Madagascan relatives, was a fully terrestrial animal occupying a niche similar to that of many modern lizards in semi-arid environments. This is in accord with the reconstructed palaeo-environment (see above) and with aspects of the preservation which may provide evidence of behaviour.

The juveniles of some modern species of viviparous lizards, e.g. skinks, are known to huddle together with very similar intertwining and side-by-side disposition. These aggregations involve members of a single brood and are usually found in confined cavities beneath fallen logs or within underground burrows (Shine 1994). Under warm, semi-arid climatic conditions the advantages of such behaviour could be improved diurnal thermoregulation (Gregory 1982) and more efficient aestivation during drought (Seidel 1978).

Published reports of monospecific juvenile aggregation in other groups of fossil reptiles involve Cretaceous ornithopod dinosaurs, namely hypsilophodontids (Horner 1984), *Tenontosaurus* (Forster 1990) and hadrosaurs (Horner and Makela 1979), many of which have been found in association with nests and eggshells. To date, no eggs or nesting sites have been found in the

Beaufort Group although burrow casts containing curled-up skeletons of the small dicynodont *Diictodon* do occur in the vicinity of the younginid locality (Smith 1987*b*). Interestingly, an aggregation of ten juvenile skeletons of *Diictodon* (SAM K1650) was found within 100 m of the younginids and ten more isolated juvenile *Diictodon* skulls occurred along the 1300 m cliff section (Text-fig. 2). The relatively common preservation in the proximal floodplain facies of articulated juvenile skeletons belonging to more than one tetrapod group may indicate that this was a preferred 'nesting' area. However, the wide range of disarticulation classes amongst the rest of the fossil assemblage and the 'clustering' of fossils with comparatively unweathered bone surfaces suggests that the periodicity of flood events and the net floodplain accretion rate were the major factors determining the preservation of skeletons. Floodplain accretion rates of the strata that host the juvenile aggregations range from 14 mm/y in topographical lows to 9 mm/y on the flats (Smith 1993). These rates are high enough to suggest regular, possibly seasonal, flooding of the proximal floodplains and it is proposed that the greater frequency of overbank flows resulted in the increased preservation of juveniles in these sediments.

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